

The evolutionary significance of colour, colour patterns and fluorescence in scorpions

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The evolutionary significance of colour, colour patterns and fluorescence in scorpions. - From a survey of the scorpion faunas of North Africa, Namibia, Baja California, tropical South America and the Caribbean, it is concluded that the principal function of the colour of scorpions is crypsis - pale or variegated in open savanna and deserts, dark in dense vegetation and rain-forest. Probable explanations are given for the existence of species that are exceptions to this rule. The possible functions of fluorescence in ultra-violet light are also discussed.

Key-words: Scorpion - colour - colour patterns - crypsis - fluorescence - ultra-violet light.

INTRODUCTION

The colour and colour patterns of scorpions have often attracted the attention of biologists, mostly in relation to taxonomic studies (e.g. KRAEPELIN 1899; POCOCK 1902; VACHON 1952; LOURENÇO 1980; LAMORAL 1979). The ecological significance of colours and patterns are, however, much less well understood (CLOUDSLEY-THOMPSON 1993a, b). Moreover, biologists have long disregarded the importance of ontogenic variability in colours and colour patterns. This leads to errors in the definition both of species and of natural populations. Only recently has this point begun to be elucidated (LOURENÇO 1980, 1983), and it is now realized that, in many species, juveniles and adults have totally different colour patterns. The coloration of scorpions ranges from almost black to very pale yellow, while some troglobitic species such as *Sotanochactas elliotti* (Mitchell), are almost totally unpigmented.

According to CLOUDSLEY-THOMPSON (1961, 1993a, b), scorpions may have evolved nocturnal behaviour patterns in response to predation. Moreover, it is gene-

rally assumed that their colours and colour patterns are nearly always associated with crypsis (POLIS 1990; CLOUDSLEY-THOMPSON 1993a, b). Thus, most of the scorpions that live in open areas such as deserts and dry savannas are pale, whereas those living in dense vegetation and rain-forests are dark and often black.

A question arises, however, as to why several exceptions to this rule can be observed. The object of our paper is to answer this question at least partially. We base our arguments on examples from well studied faunistic regions such as North Africa, Namibia, Baja California, tropical South America and the Caribbean.

Another characteristic of scorpions, which is shared with other orders of Arachnida, is the emission of a fluorescent glow when exposed to ultra-violet light. This has been demonstrated in numerous species belonging to all families (CLOUDSLEY-THOMPSON 1978) but its function is little understood. This phenomenon, too, will be discussed in the present paper.

1 – EXAMPLES FROM DESERT FAUNAS

Most of the species present in desert regions are pale yellow and unpigmented. Exceptions can, however, be found. For example, in the North African deserts, most varieties of *Scorpio maurus* (Linnaeus) are dark, which is in accordance with the general coloration of the family Scorpionidae. Among Buthid scorpions, species such as *Orthochirus innesi* Simon, *Hottentotta frauzweneri* (Birula), *Buthus maroccanus* Birula and *Microbuthus fagei* Vachon, show dark pigmentation. The same applies to species of the genus *Butheoloides* Hirst. In this case, however, only one species, *Butheoloides maroccanus* Hirst, lives in truly desert areas.

Another marked exception is found in the genus *Androctonus* which presents several dark coloured species, *A. hoggarensis* (Pallary), *A. aeneas* Koch, *A. crassicauda* (Olivier), *A. mauretanicus* (Pocock) and *A. sergenti* Vachon, whereas only two are pale yellow, *Androctonus australis* (Linnaeus) and *A. amoreuxi* (Aud. & Sav.). Other species from North Africa, which belong to the genera *Buthacus*, *Cicileus*, *Buthiscus*, *Lissothus*, *Leiurus*, *Compsobutuhus* and *Buthus*, are all pale (VACHON 1952).

In other desert regions, such as Saudi Arabia and Oman (VACHON 1977, 1979), the scorpions are also usually pale in colour. The same exceptions occur there in species of *Androctonus*, and in *Orthochirus innesi* but even Scorpionidae such as *Hemiscorpius arabicus* Pocock, *Hemiscorpius maindroni* Simon and *Scorpio maurus kruglovi* Birula are lighter in colour than in North Africa and are dark yellow.

In Namibia, a dichotomy associated with colour pattern and phylogenetic relationship is to be observed even more clearly. Buthidae of the genera *Hottentotta*, *Karasbergia*, *Parabuthus* and *Uroplectes* are, in general pale, whereas the Scorpionidae are dark. An exception in the last family is *Hadogenes phyllodes* (Thorell) which is paler than the other species (LAMORAL 1979).

In the North American deserts, and especially in Baja California, species of Buthidae and Vaejovidae are pale, whereas these of Diplocentridae are rather dark. Some exceptions are *Hadrurus piuteri* Stahnke, *Nullibrotheas allenii* Wood, *Vaejovis*

gigantaensis Williams, *Vaejovis harbisoni* Williams and *Vaejovis jaussi* Williams which are dark (WILLIAMS 1980). Finally, in the arid regions of Australia, species belonging to the genus *Urodacus* (Scorpionidae), are pale yellow (KOCH 1977).

II — EXAMPLES FROM OPEN VEGETATION FORMATION FAUNAS

Some of the formations of open vegetation best studied are those of the South American savannas, i.e. Chaco, Cerrados and Llanos, and those of arid South America such as the Caatingas in North East Brazil (LOURENÇO 1982, 1990a, 1994; LOURENÇO & EICKSTEDT 1988). The scorpion faunas of the African savannas are less well known and still present many gaps in knowledge (LOURENÇO & SASTRE 1988). For this reason, in the present paper, examples have been cited mainly from South America.

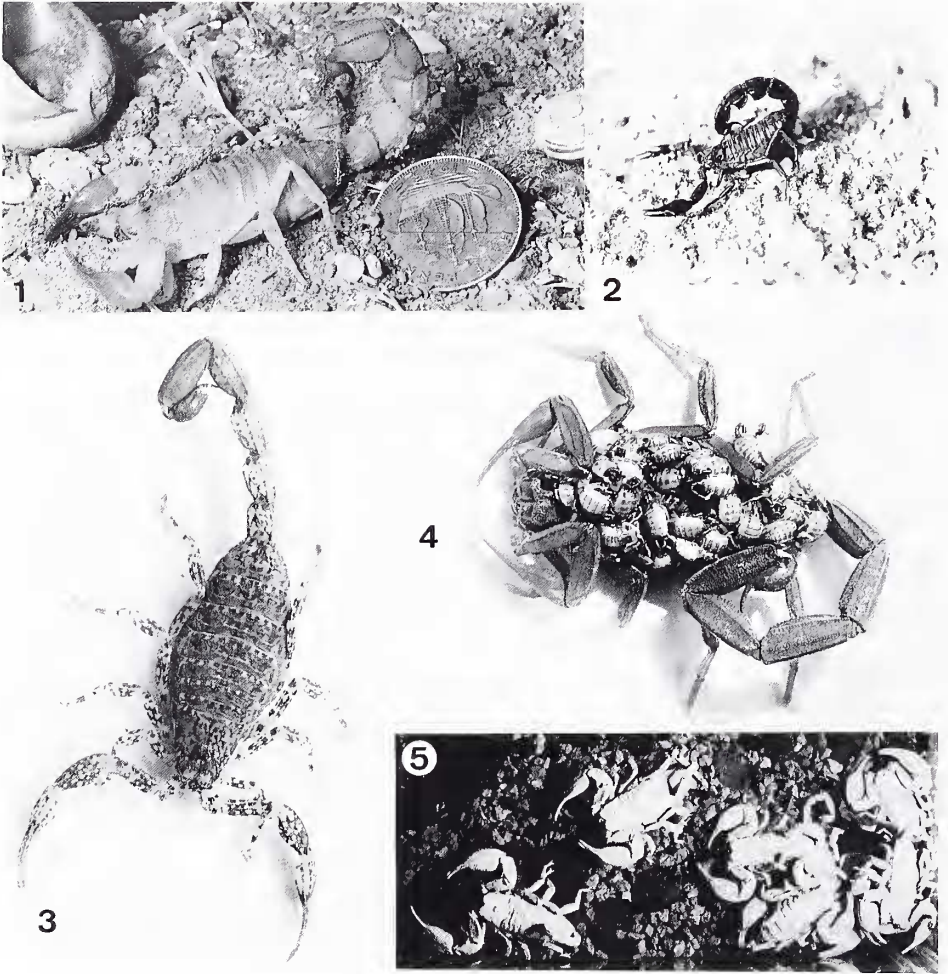
Only two scorpion families, the Bothriuridae and the Buthidae, are present in the region lying between the North of Argentina, and North East Brazil. This includes Paraguay and the Central region of Brazil and is known as "the diagonal of Brazilian open formations" (DE MARTONNE 1935; LOURENÇO 1990a). Almost all the species of Buthidae found here are pale, whereas those of the Bothriuridae are usually dark. Some exceptions occur in both cases, however. Thus, of the Buthids, *Rhopalurus acromelas* Lutz & Mello-Leitão and *Tityus bahiensis* (Perty) are rather dark while, of the Bothriuridae, *Bothriurus rochai* Mello-Leitão and *Brachistosternus* (*M.*) *ferrugineus* (Thorell) are pale.

All species of *Rhopalurus* are adapted exclusively to open vegetation. Their colour ranges from yellow in *Rhopalurus rochae* Borelli to brown-yellow in *Rhopalurus agamemnon* (Koch). Even *Rhopalurus amazonicus* Lourenço, which lives in patchy areas of savanna enclave within the Amazonian rain forest, is yellow (LOURENÇO 1982a, 1986).

The species of *Tityus* living in open vegetation show two major types of coloration. In the first there are species ranging from yellow, as *Tityus stigmurus* (Thorell) or reddish-yellow, as *Tityus trivittatus* Kraepelin, grading into brown-yellow as in *Tityus fasciolatus* Pessôa. In the second group, a dark variegated colour pattern is found over a yellow or a clear colour base. This pattern, which can be observed in species such as *Tityus paraguayensis* Kraepelin and *Tityus matto-grossensis* Borelli, is also present in the other species of *Tityus* belonging to the same phylogenetic group and living in dry areas or rain forest (LOURENÇO 1992). We will discuss this further below. A similar pattern is also to be seen in species of the genera *Ananteris* and *Microtityus* which likewise inhabit both open and forested regions (LOURENÇO 1982b; LOURENÇO & EICKSTEDT 1983).

III — EXAMPLES FROM FOREST FAUNAS

The scorpions of the forest ecobiome are generally dark brown or black. This is the case in species of the families Scorpionidae, Ischnuridae, Chactidae, Chaerilidae, Diplocentridae and Buthidae. Few examples of pale species can be found

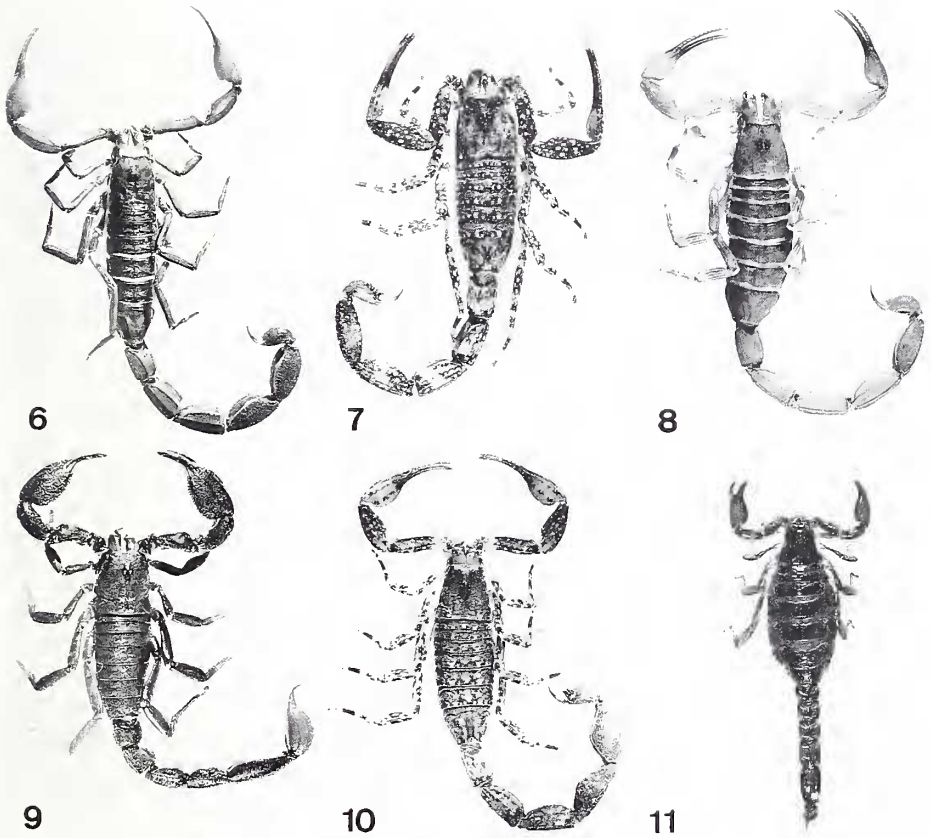


FIGS 1-5

Fig. 1. *Androctonus australis* an yellow scorpion from desert regions of North Africa. Fig. 2. *Androctonus crassicauda* a dark scorpion from desert regions of North Africa and Middle East. Fig. 3. *Tityus matogrossensis*, a variegated scorpion from Brazilian Savannas. Fig. 4. *Centruroides gracilis* a dark scorpion from both dry savannas and forests from the U.S.A. to South America. Fig. 5. *Opisthacanthus cayaporum* a dark scorpion from Brazilian Savannas, under ultra-violet light.

in the first two families. *Opisthacanthus valerioi* Lourenço, from Cocos Island is one of the exceptions, as it is yellow. Some other instances occur in Africa both of Scorpionidae and Ischnuridae with dark yellow-brown coloration.

Species of Chactidae (at least of Chactinae), living in forests, are uniformly dark probably as an adaptation to the vegetation. *Chactas keyserlingi* Pocock, which



FIGS 6-11

Fig. 6. *Tityus metuendus*, a black scorpions from Amazonia. Fig. 7. *Tityus metuendus*, juvenile with a characteristic variegated colour. Fig. 8. *Tityus raquelae*, a pale scorpion from Amazonia. Fig. 9. *Brotheas amazonicus* a dark scorpion from Amazonia. Fig. 10. *Tityus silvestris*, a variegated scorpion from Amazonia. Fig. 11. *Bothriurus araguayae* a dark scorpion from Brazilian Savannas.

is found in arid regions of Colombia; is the only known example of a species of Chactinae living in an arid region, but this species is also dark (LOURENÇO 1991).

Species of the families Chaerilidae and Diplocentridae, are usually red-brown to dark-brown. They can be found in both open vegetation and forested regions. Species of Buthidae living in forests are almost invariably dark brown or black; for example, several *Tityus* and *Centruroides* spp. of South, Central and North America. A common colour pattern, variegated dark brown over a pale base, is to be seen in species of open vegetation. This pattern is very common among species of the genera *Ananteris* and *Microtityus* in the Neotropics, as well as in species of the genera *Isometrus* and *Lychas* in Africa, the Indo-Malasyan region and Australia. Moreover,

the same pattern is also seen in the juvenile forms of both *Tityus* and *Centruroides* spp. that are dark brown or black when adult (Lourenço 1983). We shall return to this point in the Discussion.

Several interesting exceptions, provided by species of *Tityus* and *Centruroides* living in forests in South and Central America, can be listed: *Tityus engelkei* Pocock from Santa Marta in Colombia is yellow. *Tityus sastrei* Lourenço & Florez and *Centruroides margaritatus* from Pacific coastal forests in Colombia and Ecuador are yellow-red to yellow-brown. *Tityus gasci* Lourenço, *Tityus blanci* Lourenço, *Tityus strandi* Werner, *Tityus jussarae* Lourenço (this is a troglaxene species), *Tityus melanostictus* Pocock, *Tityus discrepans* Pocock and *Tityus filodendron* Gonzalez-Sponga, from the Amazonian region, are mostly yellow or sometimes reddish-yellow.

In other forests such as the Atlantic coastal forest of Brazil, no pale or yellow species are known. The colours and patterns are invariably dark brown, black or variegated, as in *Tityus brazilae* Lourenço & Eickstedt and *Tityus pusillus* Pocock. African, Asian and Australian forests providing examples of pale species are poorly known, but it is certain that exceptions, such *Hottentota hottentota* (Fabricius), which are found both in arid regions and tropical forest, are also present there.

FLUORESCENCE IN ULTRA-VIOLET LIGHT

It has long been known that scorpions fluoresce very strongly when exposed to ultra-violet light in the range 320–400 nm (3,200–4,000 Å), which facilitates their study and collection in the field (SISSOM *et al.* 1990). Fluorescence in ultra-violet light also occurs with other Arachnida (and other Arthropoda), especially Solifugae, but its significance is not understood (CLOUDSLEY-THOMPSON 1978). It gradually fades when scorpions are maintained continuously in ultra-violet light and, after about a week, disappears entirely. If a piece of black adhesive tape has first been attached to the opisthosoma of a scorpion, after it has lost the ability to fluoresce only that portion of the body which had previously been covered will show fluorescence when the tape is removed. The reaction occurs in the hyaline exocuticle and the substance which causes fluorescence is soluble in alcohol: it can be crystallised out (C. Constantinou, *in litt.*). Water loss in dry air at 23°C from an adult living *Androctonus crassicauda* (Olivier) doubled over a period of 15 days when the scorpion was maintained under ultra-violet light (700 $\mu\text{W cm}^{-2}$) in the laboratory (CONSTANTINOU & CLOUDSLEY-THOMPSON 1985).

Fluorescence in ultra-violet light is known for only a small number of day-active Arachnida including spiders (LOURENÇO *et al.* 1988; LOURENÇO 1990b), while new-born scorpions do not fluoresce until their cuticle has sclerotized. According to F.H. Koehler (cited by HJELLE 1990), it may be possible for a scorpion to detect very low intensities of light at certain wavelengths. This may explain the extreme sensitivity to light of the eyes of *Androctonus australis* (L.) reported by FLEISSNER & FLEISSNER (1985). In any case, there is no evidence to show that scorpions react to one another visually, either when mating or when one individual preys upon another. We

doubt whether the basic function of the fluorescent chemical is waterproofing, or that it makes scorpions attractive to insect prey. It is possible, however, that in daylight scorpions could absorb a degree of radiation that might have a deleterious effect upon the cuticles, just as sunlight does on many man-made polymers (CLOUDSLEY-THOMPSON 1978).

DISCUSSION

From the examples presented above, it seems logical to suggest that the colours and colour patterns of scorpions have a primarily cryptic significance. They seem also to be associated with phylogenetic lineage. The species of Chactidae (at least of Chactinae), as well as of most Scorpionidae and most Diplocentridae, are dark, regardless of the habitat in which they live. It is reasonable to assume that a dark colour is cryptic in forests and dense vegetation, and that pale colours and yellow are cryptic in deserts and open vegetation. However, the third type of coloration observed, variegated colours, seems to be effective in both forests and open vegetation since species presenting this pattern occur in both. Moreover, the juveniles of black species such as *Tityus cambridgei* Pocock, *Tityus metuendus* Pocock and *Centruroides gracilis* (Latreille), show a variegated pattern almost until they became adult. Variegated colours probably act as camouflage: They are not found in desert species.

What possible explanation can be given for the presence of dark species in deserts and of pale or yellow species in forests? Most lineages of scorpions are very old (SISSOM 1990), and colour patterns have been established in different taxa over a very long period of time. The evolution of these colours is undoubtedly associated with the ecological requirements of the environment. It is possible that scorpion species will naturally evolve dark or pale colours in a given amount of time, which is not necessarily short. The colours and patterns observed today probably evolved at moments of paleohistory when different environments experienced long periods of stability (most existing scorpion groups had undoubtedly evolved before the Cenozoic). In more recent times, especially during the Pleistocene and Holocene, rain-forests and savannas experienced considerable vicissitudes in their climatological conditions. Several periods of expansion and contraction, both of rain-forests and of arid savannas, are known to have occurred in Amazonia during the Pleistocene and Holocene (HAFFER 1969; PRANCE 1982, 1985; LOURENÇO 1987).

According to PRANCE (1982, 1985), the reduction of forest to small patches affected the organisms existing there in one of three ways: (a) they became extinct; (b) they survived with little or no evolutionary changes, or; (c) they began to differentiate and even to speciate in refugia. It seems logical to assume that situations (a) and (b) took place most frequently. Black species therefore remained in forested refugia: when the forest expanded again, they merely recolonised the whole environment. On the other hand, during periods of forest expansion, some pale species, which had previously colonised dry savanna formations, may possibly have evolved rapidly in terms of their behaviour and physiology so that they were able to survive in a forested environment.

This rapid evolution was not followed by any modification of colour, which probably takes much longer. It is possible that pale forest species may be less well adapted in terms of crypsis, and that they may suffer negative selection by predators. However, scorpions are nocturnal, and even if forest species are much less nocturnal in their activity than are desert species (CLOUDSLEY-THOMPSON 1981), forests are so dark that this vegetation and deserts, a possible readaptation from a previously forested environment may also be the explanation. However, in this case they would be much more exposed to predation because they lack cryptic protection unless, of course, the dark coloration is aposematic under these conditions (CLOUDSLEY-THOMPSON 1993*a, b*).

The different examples of coloration in scorpions presented in this paper are not exhaustive. Our object has been to try to explain the significance of coloration and pattern, and the causes of some of the exceptions to the general principles proposed. We have been less successful in attempting to explain the function of fluorescence in ultra-violet light.

REFERENCES

- CLOUDSLEY-THOMPSON, J.L. 1961. Adaptive functions of circadian rhythms. *Cold Spring Harbor Symposia on Quantitative Biology* (1960), 25: 345–355.
- CLOUDSLEY-THOMPSON, J.L. 1978. Biological clocks in Arachnida. *Bulletin of the British Arachnological Society* 4(4): 184–191.
- CLOUDSLEY-THOMPSON, J.L. 1981. A comparison of rhythmic locomotory activity in tropical forest Arthropoda with that of desert species. *Journal of Arid Environment* 4(4): 327–334.
- CLOUDSLEY-THOMPSON J.L. 1993*a*. The adaptational diversity of desert biota. *Environmental Conservation* 20(3): 227–231.
- CLOUDSLEY-THOMPSON, J.L. 1993*b*. Successful desert animals — scorpions, beetles and lizards. *Libyan Studies* 24: 143–156.
- CONSTANTINOU, C. & J.L. CLOUDSLEY-THOMPSON, 1985. Transpiration in ultra-violet light from a scorpion. *News letters of the British Arachnological Society* N° 44: 7.
- DE MARTONNE, E. 1935. Problèmes des régions arides sud-américaines. *Annales de Géographie* 44: 1–27.
- FLEISSNER, G. & G. FLEISSNER, 1985. Neurobiology of a circadian clock in the visual system of scorpions. *In*: F.G. BARTH (ed.): Neurobiology of Arachnids. *Springer-Verlag, Berlin, Heidelberg, New York, Tokyo*: pp. 351–375.
- HAFFER, J. 1969. Speciation in Amazonian forest birds. *Science* 165: 131–137.
- HIELLE, J.T. 1990. Anatomy and morphology. *In*: G.A. POLIS (ed.): The Biology of Scorpions. *Stanford University Press, Stanford*: pp. 9–63.
- KOCH, L.E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australian-Papuan scorpions. *Records of the Western Australian Museum* 5(2): 83–367.
- KRAEPELIN, K. 1899. Scorpiones und Pedipalpi. *In*: *Das Tierreich* 8: 1–265.
- LAMORAL, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23(3): 497–784.
- LOURENÇO, W.R. 1980. Contribution à la connaissance systématique des Scorpions appartenant au "complexe" *Tityus trivittatus* Kraepelin, 1898 (Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e sér., 2, sect. A, (3): 793–843.

- LOURENÇO, W.R. 1982a. Révision du genre *Rhopalurus* Thorell, 1876 (Scorpiones, Buthidae). *Revue Arachnologique* 4: 107–141.
- LOURENÇO, W.R. 1982b. Révision du genre *Ananteris* Thorell, 1891 (Scorpiones, Buthidae) et description de six espèces nouvelles. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e sér., 4(A1–2): 119–151.
- LOURENÇO, W.R. 1983. Importance de la pigmentation dans l'étude taxonomique des Buthidae néotropicaux (Arachnida, Scorpiones). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e sér., A(2): 611–618.
- LOURENÇO, W.R. 1986. Biogéographie et phylogénie des Scorpions du genre *Rhopalurus* (Scorpiones, Buthidae). *Mémoires de la Société royale belge d'Entomologie* 33: 129–137.
- LOURENÇO, W.R. 1987. Les modèles évolutifs des Scorpions néotropicaux et la théorie des refuges forestiers du Pléistocène. *Compte-rendu des séances. Société de biogéographie* 63(3): 75–88.
- LOURENÇO, W.R. 1990a. Caractéristiques biogéographiques de la Caatinga brésilienne. Associations avec le Chaco et d'autres formations végétales ouvertes de l'Amérique du Sud. L'exemple des Scorpions. *Compte-rendu des séances. Société de biogéographie* 66(4): 149–169.
- LOURENÇO, W.R. 1990b. A new species of *Psecunia* from Colombia (Araneae, Oxyopidae). *Caldasia* 16(77):193–195.
- LOURENÇO, W.R. 1991. Les Scorpions (Chelicerata) de Colombie. II. Les faunes des régions de Santa Marta et de la Cordillère Orientale. Approche biogéographique. *Senckenbergiana Biologica* 7(4–6): 275–288.
- LOURENÇO, W.R. 1992. Biogéographie des espèces du groupe naturel "*Tityus clathratus*" (Chelicerata, Scorpiones, Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e sér., 14(A2): 473–481.
- LOURENÇO, W.R. 1994. Synopsis de la faune des Scorpions du Paraguay. *Revue suisse de Zoologie* 101(3): 677–684.
- LOURENÇO, W.R. & V.R.D.V. EICKSTEDT 1983. Présence du genre *Microtityus* (Scorpiones, Buthidae) au Brésil. Description de *Microtityus vanzolinii* sp. n. *Revue Arachnologique* 5(2): 65–72.
- LOURENÇO, W.R. & V.R.D.V. EICKSTEDT, 1988. Sinopse das espécies de *Tityus* do nordeste do Brasil com a redescricao de *Tityus neglectus* Mello-Leitão (Scorpiones, Buthidae). *Revista brasileira de zoologia* 5(3): 399–408.
- LOURENÇO, W.R., J. KOVOOR & A. MUÑOZ-CUEVAS, 1988. Observations on spiders in ultraviolet light. *TUB-DOKUMENTATION Kongresse und Tagungen*, Heft 38, Berlin 1988: pp. 342–349.
- LOURENÇO, W.R. & C. SASTRE 1988. Les savanes néotropicales: caractéristiques écologiques et biogéographiques. Exemples de modalités de peuplement chez les Scorpions et chez les Phanérogames. *Compte-rendu des séances. Société de biogéographie* 64(2): 43–77.
- POCOCK, R.I. 1902. Arachnida, Scorpiones. In: *Biologia centrali-americana. Taylor and Francis London*: pp. 1–71.
- POLIS, G.A. 1990. Ecology. In: G.A. POLIS (ed.). *The Biology of Scorpions. Stanford University Press, Stanford*: pp. 247–293.
- PRANCE, G.T. 1982. Forest refuges: Evidence from woody angiosperms. In: G.T. PRANCE (ed.), *Biological diversification in the tropics. Columbia University Press, New York*: pp. 137–158.
- PRANCE, G.T. 1985. The changing forests. In: G.T. PRANCE & T.E. LOVEJOY (eds.): *Amazonia. Pergamon Press, London*: pp. 146–165.
- SISSOM, W.D. 1990. Systematics, biogeography, and paleontology. In: G.A. POLIS (ed.): *The Biology of Scorpions. Stanford University, Stanford*: pp. 64–160.

- SISSOM, W.D., G.A. POLIS & D.D. WATT 1990. Field and laboratory methods. *In*: G.A. POLIS (ed.), *The Biology of Scorpions*. Stanford University Press, Stanford: pp. 445–461.
- VACHON, M. 1952. Etudes sur les Scorpions. *Institut Pasteur Algérie, Alger*: 482 p.
- VACHON, M. 1977. Scorpions. *In*: The scientific results of the Oman Flora Survey 1975. *Journal of Oman Studies, Special Report*: pp. 209–217.
- VACHON, M. 1979. Arachnids of Saudi Arabia Scorpiones. *Fauna of Saudi Arabia* 1: 30–66.
- WILLIAMS, S.C. 1980. Scorpions of Baja California, Mexico, and adjacent Islands. *Occasional Papers of the California Academy of Sciences* 135: 1–127.